THE FOSSIL RECORD OF THE EPACRIDACEAE

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Abstract

Fossil pollen and macrofossils of Epacridaceae are uncommon and are mainly known from Tasmania and other parts of south-eastern Australia. Most epacrids have generalised ericalean pollen although the pollen of some genera is distinctive. Ericalean pollen is known from the late Cretaceous. The first occurrence of *Paripollis orchesis* pollen, which is consistent with some extant *Epacris* species, probably means that Epacridaceae, and possibly the tribe Epacrideae, had differentiated by the Middle Eocene.

The fossil record at present provides minimum ages of the first occurrences of major subfamilial taxa. Macrofossils of subfamily Richeoideae and of several morphotypes of the tribe Epacrideae are known from the Early Oligocene. Tribe Cosmelieae pollen and macrofossils are known from the Early Pleistocene, and are probably *Sprengelia*. The oldest Australasian fossils of tribe Styphelieae are leaves in latest Oligocene-Early Miocene parts of the Latrobe Valley coal. Endocarps identified as Epacridaceae from the Eocene of England need further investigation. Pollen of *Monotoca*, or a close relative, is known from the mid-Miocene. Possible *Trochocarpa* leaves occur in Late Oligocene/Early Miocene sediments, and fossil leaves indistinguishable from the extant Tasmanian rainforest species, *T. gunnii* and *T. cunninghamii*, are known from the Early Pleistocene in Tasmania.

Key words: Epacridaceae, macrofossils, microfossils, Cretaceous, Cainozoic.

Running head: The fossil record of the Epacridaceae

Introduction

The vegetation of much of non-arid of Australia is dominated by a scleromorphic flora, but the fossil record of most of the major taxonomic groups, with the main exception of Proteaceae, is poor (Carpenter, Hill and Jordan, 1994; Hill, 1994; Macphail *et al*., 1994). Epacridaceae are prominent in the extant scleromorphic flora, and recently our knowledge of both macrofossils and microfossils of this family has increased significantly. This work summarises the fossil record, and includes some new macrofossil records.

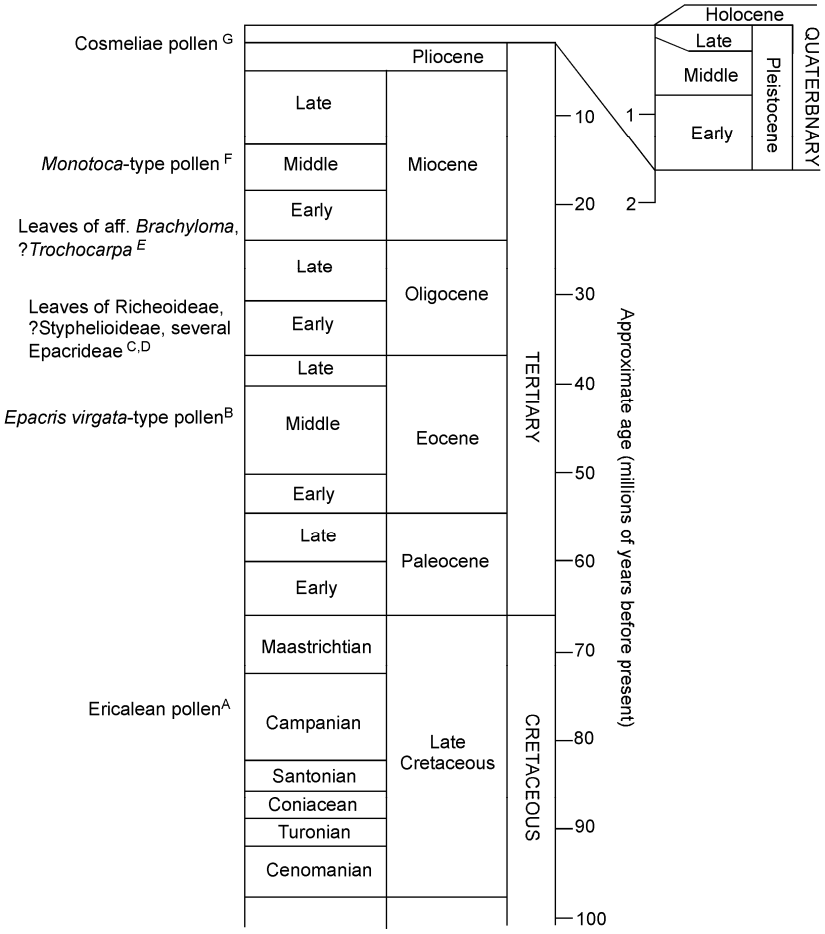


Fig. 1. Time scale showing major events in the fossil record of Epacridaceae, and approximate absolute ages (after Haq and Eysinga 1987 except for the Quaternary which follows Harland *et al.* 1990). Data from A Dettman (1994), B Macphail *et al.* (1994), C Jordan *et al.* (1995), D this work, E Blackburn (1985), F Martin (1993) and G M. K. Macphail personal communication.

Methods

In addition to previously recorded epacrid fossils, fossil leaves extracted from sediments at Lea River (Early Oligocene: Carpenter *et al*., 1994; the time scale followed is shown in Fig. 1), Huskisson/Marionoak Divide and Regatta Point (Early Pleistocene: Hill and Macphail, 1985;

Macphail, Jordan and Hill, 1993; P. A. Augustinius , personal communication 1995) and Regency (Middle Pleistocene: Jordan, 1992) were assessed to determine if there were any epacrids present at these sites (Fig. 2). Microphylls from the Monpeelyata sediments (Late Oligocene/Early Miocene: Macphail *et al*., 1991), many of which Hill and Gibson (1986) considered were probably Epacridaceae, were reassessed. Macrofossils were extracted from these sediments, prepared and identified following the methods described in Jordan and Hill (1995). The intra-familial classification used here follows Watson (1967), which appears to broadly conform to natural groupings (Powell, Chapman and Doust, 1987).

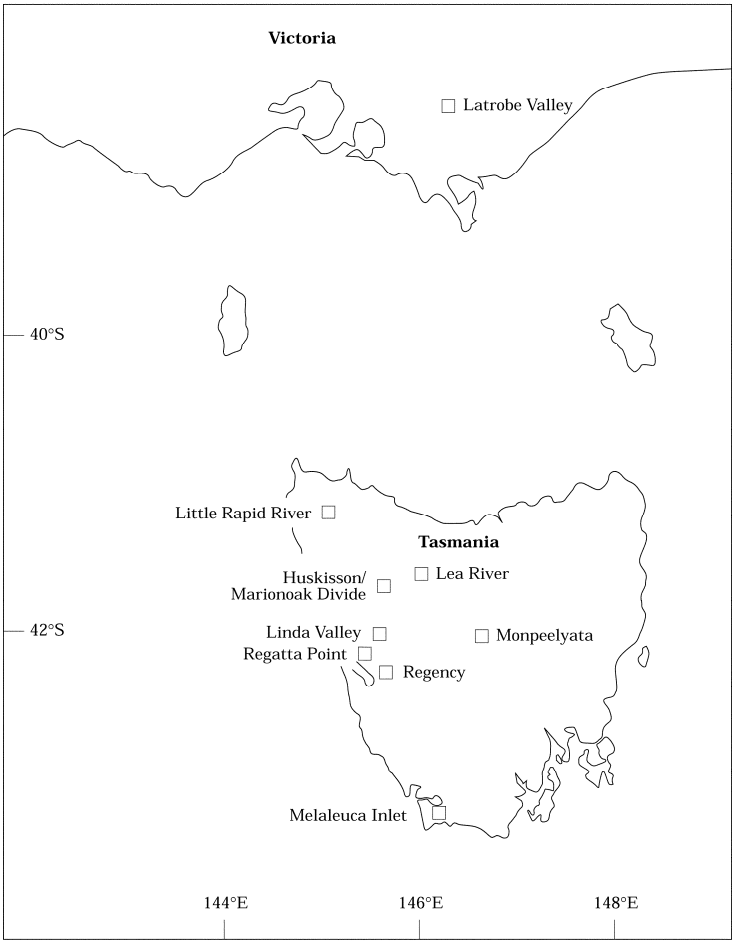


Fig. 2. South eastern Australia showing the location of fossil deposits mentioned in the text.

Results

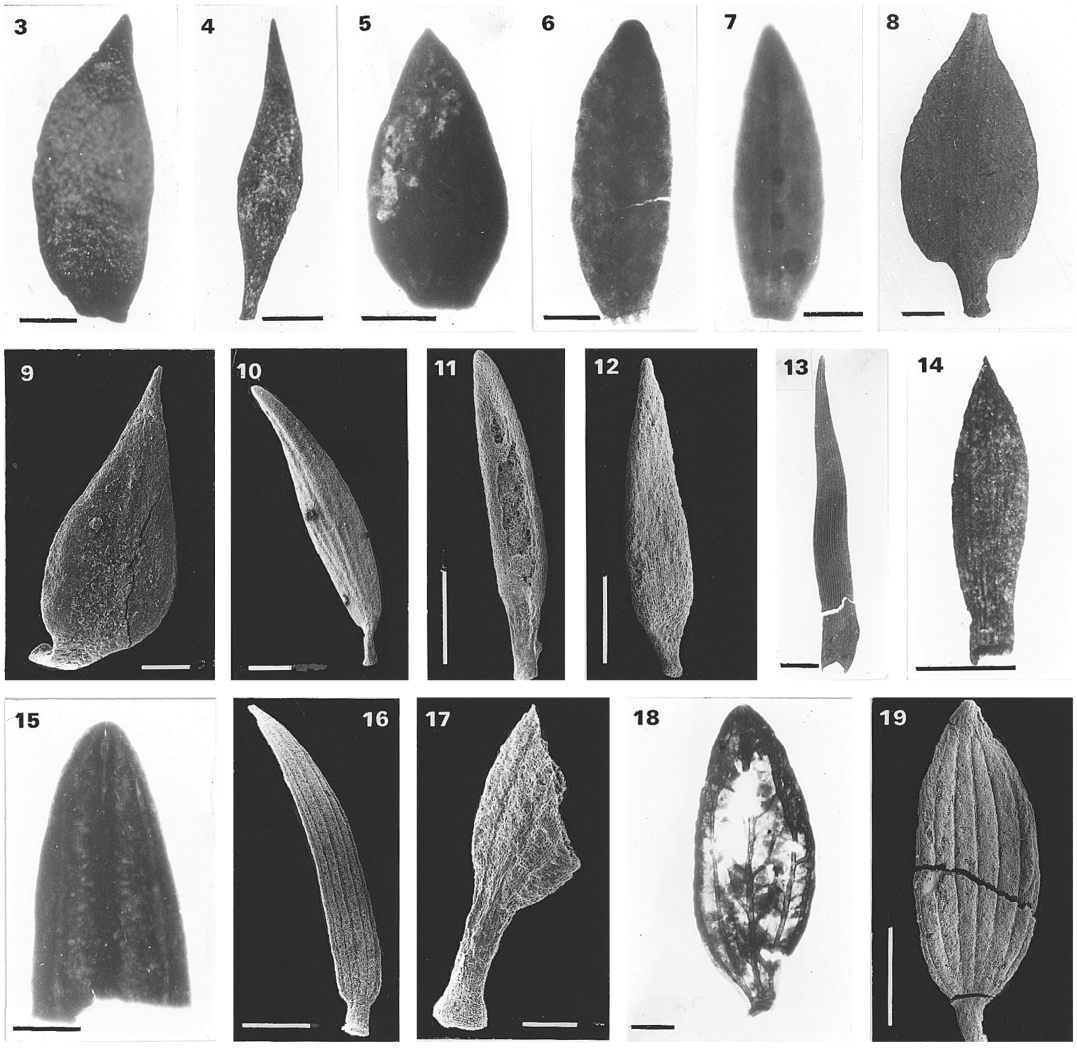
The Lea River sediments contain at least one species of tribe Epacrideae (Fig. 5). The Monpeelyata sediments include at least two morphotypes consistent with Epacrideae (Figs 6 and 7) and others consistent with many Styphelieae (Fig. 16), based on leaf shape, parallel venation and cuticle, although their cuticles are poorly preserved. Some leaves at Monpeelyata have venation with strong, high angle, reticulate veins connecting the longitudinal veins (Fig. 18) and are similar to *Trochocarpa*, but affinity to other Epacridaceae cannot be excluded, since their cuticles are not well

preserved. At least one *Epacris* species, two species of either *Epacris* or *Archeria* (Figs 8-10), whole Richeoideae leaves (Fig. 13), *Sprengelia incarnata*-type foliage, Styphelieae leaves consistent with *Cyathodes* and a few other genera (Fig. 16) and leaves of *Trochocarpa* consistent with the extant Tasmanian species *T. cunninghamii* and *T. gunnii* (Fig. 19) occur in the Regatta Point sediments (Jordan, 1992). Styphelieae leaves (Fig. 17) and at least two morphotypes of Epacrideae (Figs 11-12) occur in the Huskisson/Marionoak Divide sediments.

The fossils described above and all previously recorded Tertiary and Pleistocene macrofossils of Epacridaceae are listed in Table 1.

Table 1. Macrofossils of Epacridaceae and possible Epacridaceae, based on Reid and Chandler (1933)[A], Jordan and Hill (1995)[B], this study[C], Hill and Gibson (1986)[D], Blackburn (1985)[E], Jordan (1992)[F], and Jordan *et al.* (1991)[G].

Taxon	**Modern affinity**	**Site**	**Age**
Leucopogon quadrilocularis	?Styphelieae	London Clay, England[A]	Eocene
Epacriphyllum mesibovii	Epacrideae	Little Rapid River[B]	Early Oligocene
E. macphailii	Epacrideae	"	"
Richeaphyllum jonesii	Richeoideae	"	"
? Styphelieae	Styphelieae	"	"
Epacriphyllum sp.	Epacrideae	Lea River[C]	"
Epacriphyllum sp.	Epacrideae	Monpeelyata[C,D]	Late Oligocene/Early Miocene
cf. *Trochocarpa*	?*Trochocarpa*	"	"
cf. Styphelieae	?Styphelieae	"	"
Brachyloma cf. *depressa*	*Brachyloma* etc	Latrobe Valley[E]	"
Epacris cf. *heteronema*	*Epacris*	Regatta Point[C,F]	Early Pleistocene
Epacriphyllum sp. 1	*Epacris*, *Archeria*	"	"
Epacriphyllum sp. 2	*Epacris*, *Archeria*	"	"
Richea cf. *milliganii*	*Richea* spp	"	"
cf. *Cyathodes juniperina*	*Cyathodes*, *Lissanthe* etc.	"	"
Trochocarpa cf *gunnii*	*Trochocarpa* spp	"	"
Epacriphyllum sp. 3	*Epacris*, *Archeria*	Huskisson/Marionoak[C]	"
Epacriphyllum sp. 4	*Epacris*, *Archeria*	"	"
Styphelieae	Styphelieae	"	"
Epacriphyllum	*Epacris*, *Archeria*	Regency[C,F]	Middle Pleistocene
Trochocarpa cf *gunnii*	*Trochocarpa* sp	"	"
Epacris heteronema	*E. heteronema*	Melaleuca Inlet[G]	Late Pleistocene
Epacriphyllum	*Epacris*, *Archeria*	"	"
Monotoca cf *glauca*	*Monotoca* spp	"	"
Sprengelia incarnata	*S. incarnata*	"	"



Figs 3-19. Fossil leaves of Epacridaceae. Fig. 3. *Epacriphyllum macphailii* (Little Rapid River, Early Oligocene). Fig. 4. *Epacriphyllum mesibovii* (Little Rapid River, Early Oligocene). Fig. 5. *Epacriphyllum* sp. (Lea River, Early Oligocene). Figs 6 and 7. *Epacriphyllum* spp (Monpeelyata, Late Oligocene/Early Miocene). Figs 8-12. *Epacriphyllum* spp leaves from Early Pleistocene sediments in western Tasmania. Figs 8-10 are from Regatta Point and Figs 11 and 12 are from the Huskisson/Marionoak site. Fig. 13. *Richea* cf. *milliganii* (Regatta Point, Early Pleistocene). Fig. 14. cf. Styphelieae (Little Rapid River, Early Oligocene). Fig. 15. cf. Styphelieae (Monpeelyata, Late Oligocene/Early Miocene). Fig. 16. cf. *Cyathodes juniperina* from Regatta Point (Early Pleistocene). Fig. 17. Styphelieae from Huskisson Marionoak (Early Pleistocene). Fig. 18. cf. *Trochocarpa* (Monpeelyata, Late Oligocene/Early Miocene). Fig. 19. *Trochocarpa* cf. *gunnii* (Regatta Point, Early Pleistocene). Scale bars for Figs 3-6, 8, 10, 14, 16 and 18 = 1 mm, for Figs 7, 9, 11, 12, 15 and 17 = 0.5 mm, for Figs 13 and 19 = 2 mm.

Discussion

The origin of the Epacridaceae

Pollen tetrads of the form species, *Ericipites scabratus*, have occurred in Australasia continuously from the Campanian (Late Cretaceous) to the present (Dettmann, 1994). Many Ericalean taxa, including many Epacridaceae produce pollen similar to *Ericipites scabratus*. Dettmann (1992) considered that several Epacridaceae probably existed in south eastern Australia by the Campanian, although it is not clear from her work why these could not be Ericaceae.

Evidence for the differentiation of the Epacridaceae, and probably of the tribe Epacrideae, is stronger by the Middle Eocene, when *Paripollis orchesis* (*Epacris virgata*-type), which is consistent with some extant *Epacris* species (Matthews, 1965), first appears (Macphail *et al*., 1994). The presence of two pollen types consistent with Epacridaceae demonstrates that Epacridaceae had probably differentiated by this time since at least one of these types is probably derived within the family. Macrofossils confirm that the family had differentiated by the Early Oligocene (Jordan and Hill, 1995).

Several taxa of endocarps from Eocene sediments in Europe have been identified as Epacridaceae (Chandler, 1963), including one as *Leucopogon*. The description and illustrations appear to be consistent with tribe Styphelieae, but not with any extant genus, and require further investigation. None of the distinctive pollen types of Styphelieae have been recognised from this region and time. If these endocarps are epacrids, and Styphelieae in particular, then this suggests an ancient diversification of the family.

The origin of taxa within the family

The first occurrence of *Paripollis orchesis* pollen in the Early Eocene implies that the family had evolved by this time (assuming that the tribe is monophyletic and the similarity of the fossil pollen to extant Epacrideae is not due to convergence). The *P. orchesis* pollen form is unlikely to be ancestral in this tribe since many extant Epacrideae have pollen matching the older and taxonomically more widespread *Ericipites scabratus* morphotype. The earliest macrofossils of Epacrideae are from the Early Oligocene Lea River and Little Rapid River sites (Figs 3- 5; Jordan and Hill, 1995). By the Early Pleistocene the tribe had differentiated into a wide range of forms (Figs 8-12) including *Epacris*.

The earliest fossils of Richeoideae are leaf fragments from the Early Oligocene Little Rapid River sediments (Jordan and Hill, 1995). These can be differentiated from Cosmelieae because their stomata are paracytic. All Richeoideae fossil leaves are relatively small (< 20 mm long), and there is no evidence of the distinctive large leaves found in some Richeoideae. Some *Richea* species, including *R. procera* and *R. sprengelioides*, produce distinctive tetrads with three aborted cells which first appear in the Late Pliocene Linda Valley sediments (M. K. Macphail, personal communication 1994).

Although Styphelieae are diverse and distinctive, there are few fossils. Apart from the European endocarps mentioned above, the oldest possible Styphelieae is a leaf in the Early Oligocene Little

Rapid River sediments, although its preservation is poor (Fig. 14; Jordan and Hill, 1995). Some leaves occur in latest Oligocene-Earliest Miocene sediments in the Latrobe Valley coal that are clearly Styphelieae and are consistent with *Brachyloma*, *Pentachondra*, *Choristemon* and some *Leucopogon* (Blackburn, 1985; Blackburn and Sluiter, 1994). *Trochocarpa* had probably differentiated by the Late Oligocene-Early Miocene, and had certainly differentiated by the Early Pleistocene (Table 1; Figs 18-19). Although several distinctive pollen forms occur among Styphelieae (Franks and Watson, 1963), the only Tertiary records are of *Monotoca* which first occurs in the mid-Miocene of south eastern Australia (Martin, 1993). A group of advanced genera within the Styphelieae (*Cyathodes*, *Lissanthe* etc.) had differentiated by the Early Pleistocene (Table 1).

The oldest known pollen and macrofossils of Cosmelieae are from the Early Pleistocene at the Huskisson/Marionoak Divide (M. K. Macphail, personal communication 1995) and Regatta Point (Table 1; Jordan 1992) repectively. *Sprengelia incarnata* is known from the Late Pleistocene Melaleuca Inlet sediments (Jordan *et al*., 1991).

General discussion

There are reasons to believe that Epacridaceae are under represented in the fossil record. The fossil record of dry or strongly seasonal regions, where most extant Epacridaceae occur, is poor. This is probably because preservation of plant parts mostly occurs in unweathered sediments, and because organs from plants growing outside riparian areas rarely enter environments suitable for preservation. Broadly increasing aridity starting late in the Tertiary that allowed deep weathering of sediments (e.g. Bowler, 1982) probably exacerbated this situation. The biases in macrofossil preservation towards wet environments are particularly strong. The presence of relatively easily degraded cuticles in Epacridaceae has probably also reduced the number of macrofossils, especially of Styphelieae. Cuticle chemistry can affect preservation and result in biases against taxonomic groups (Tegelaar *et al*., 1991). Cuticles are important in the identification of fossil Epacridaceae (e.g. Jordan and Hill, 1995) and are often the parts of leaves most resistant to decay, but even relatively recent fossil epacrid cuticles (e.g. at Melaleuca Inlet; Jordan *et al*., 1991) are more degraded than those of many other taxa within the sediments. Pollen from Tertiary and older sediments tends not to be distinguishable from generalised Ericalean pollen (*Ericipites scabratus*) unless it is highly distinctive. Degradation of epacrid pollen may also be a problem. The absence of distinctive pollen forms of Styphelieae until the appearance of *Monotoca* in the mid-Miocene (Martin, 1993) suggests that there may have been little diversification in this group until relatively late in the Tertiary.

The taxonomic resolution of the fossil epacrids described above is generally too weak for many ecological inferences to be drawn. Small leaved, scleromorphic Epacrideae, Richeoideae and Styphelieae, similar to many of the fossils, now grow in a wide range of habitats, including cool temperate rainforest, dry woodlands, heathlands and alpine environments. Thus, the macrofossils do not provide any evidence for the time of development of scleromorphic vegetation typical of

much of modern Australia. The macrofossils are mainly inconsistent with modern subtropical or tropical rainforest, where very small leaved Epacridaceae do not occur. They are, however, consistent with temperate climates at the time of deposition of all the sites, which is consistent with the floristics at the sites (Hill and Gibson, 1986; Macphail *et al.*, 1991, 1993; Carpenter *et al*., 1994). The small scleromorphic leaves in Early Oligocene sediments, amongst essentially rainforest floras, suggest that scleromorphy occurred in the family before the presence of extensive heathlands and woodlands.

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